THE ANNALS

AND

MAGAZINE OF NATURAL HISTORY.

[SECOND SERIES.]

" ..... per litora spargite muscum,
Naiades, et circùm vitreos considite fontes :
Pollice virgineo teneros hìc carpite flores :
Floribus et pictum, divæ, replete canistrum.
At vos, o Nymphæ Craterides, ite sub undas ;
Ite, recurvato variata corallia trunco
Vellite muscosis e rupibus, et mihi conchas
Ferte, Deæ pelagi, et pingui conchylia succo."
N. Parthenii Giannettasii Ecl. 1.

No. 43. JULY 1851.

I.—*Report upon the Researches of* Prof. MÜLLER *into the Anatomy and Development of the* Echinoderms. By THOMAS H. HUXLEY, F.R.S.

[With a Plate.]

1. MÜLLER, JOHANN. Ueber die Larven und die Metamorphose der Ophiuren. *Transactions of the Berlin Academy*, 1846.
2. MÜLLER, JOHANN. Ueber die Larven und die Metamorphose der Echinodermen. *Ibid.* 1848.
3. MÜLLER, JOHANN. Ueber die Larven und die Metamorphose der Holothurien und Asterien. *Ibid.* 1849–50.
4. MÜLLER, JOHANN. Anatomische Studien über die Echinodermen. *Müller's Archiv*, 1850, Heft ii.
5. MÜLLER, JOHANN. Berichtigung und Nachtrag zu den anatomischen Studien über die Echinodermen. *Ibid.* Heft iii.
6. MÜLLER, JOHANN. Fortsetzung der Untersuchungen über die Metamorphose der Echinodermen. *Ibid.* Heft v.
7. MÜLLER, JOHANN. Ueber die Ophiuren-larven des Adriatischen Meeres. *Ibid.* 1851. Heft i.

WE purpose in the present article to give some account of the results at which the illustrious author of the works whose titles are prefixed has arrived, in the course of a series of elaborate and patiently conducted researches in one of the most remarkable and most obscure provinces of zoological and physiological science. It is a province too in which Professor Müller is at

once Columbus and Cortez. The discoverer—he has gleaned all its riches. For it so happens that Sars, the only investigator who preceded him in the study of the development of the Echinoderms, had not the good fortune to meet with instances of the ordinary course of development, but only with a case, exceptional among the Echinoderms, but differing less from the embryogenic phænomena of other animals.

Nor are we indebted to the Professor for a widening of our embryological knowledge alone. A more exact knowledge of development involved the necessity for, and at the same time furnished the key to, a more accurate idea of the adult structure of the Echinoderms.

The ordinary Echinoderms sufficiently try the patience of the anatomist; and any one who has ever endeavoured to dissect a Holothuria, must recollect the feeling of despair with which he regarded the knotted, glairy, eviscerated mass, which was too often the reward of all his care and caution. Undaunted by the great practical difficulties, however, Prof. Müller has entered into these complementary investigations (which are contained in the fourth and fifth treatises of the foregoing list); the errors, difficulties, and contradictions which formerly infested the subject have been cleared up and rectified, and the structure of the Ophiuridæ, Asteridæ, Echinidæ, and Holothuriadæ is now capable of being reduced to broad general propositions. Without by any means claiming for the celebrated Berlin physiologist the merit of discovering facts of organization, due to Tiedemann, to Valentin, to Krohn and others, it yet cannot be denied, that under his hands these facts have first assumed their due importance, and become moulded into a consistent whole. Under his authority, then, without always caring to indicate the original sources of information, we shall give the following summary of some points of the organization of the Ophiuridæ, Asteridæ, Echinidæ and Holothuriadæ, as preliminary, and indeed necessary, to a proper comprehension of their genetic phænomena.

It is not, however, necessary for our present purpose to enter upon the anatomy of any other systems of organs than the water-vascular system, the blood-vascular system, and the nervous system.

In all the families cited, the fundamental part of these three systems consists of three distinct rings, surrounding the œsophagus; the blood-vascular ring lies innermost, the water-vascular ring next, the nervous ring outermost.

The *blood-vascular* ring, besides the branches which it gives off, is always connected with two vessels which run along opposite sides of the intestine (*Holothuria*); and in Asteridæ and Echinidæ there is a distinct tubular heart which connects the vas-

cular ring round the œsophagus with another vascular ring surrounding the anus, from which branches pass to the ovaria, &c.

Branches are given off from the principal blood-vascular ring towards the ambulacra, and in the Holothuriadæ it appears very probable that these branches accompany and indeed inclose the nerves.

The blood-vascular system is everywhere totally unconnected with the water-vascular system.

The *water-vascular* system, whose real disposition it is of great importance to understand, with reference to embryonic states, lies, it has been said, superficial to the blood-vascular system. It forms a ring, which lies close to the integument of the mouth in the Ophiuridæ and Asteridæ, surrounds the œsophagus at the base of the lantern in Echinidæ, and encircles it beneath and at some distance from the calcareous ring in the Holothuriadæ.

From this ring a series of vesicles, varying in number from four (*Ophiura*) to a hundred (*Cladolabes peruanus*), depend. These are the Polian vesicles; they open into the water-vascular ring, and appear to be in some way connected with the distribution of fluid through the water-vascular system.

Connected also with the circular water-vascular ring is the famous sand-canal, of which one or more are found in all the families enumerated. In most there is only one sand-canal, but in some Asteridæ there are several, and in *Synapta serpentina* there are a great number.

The sand-canal is a membranous tube having calcareous particles imbedded in its parietes, which are sometimes (Holothuriadæ) pierced by distinct apertures.

Now the extremity of the sand-canal may be either adherent to some part of the parietes of the animal, as in Ophiuridæ, Asteridæ, Echinidæ, or it may hang loose in the abdominal cavity, as in the Holothuriadæ. In the former case the spot to which it adheres is either entire (*Ophiura*), or perforated by many apertures which communicate with the interior of the canal (Asteridæ, Echinidæ), in which case it forms the "madreporic plate."

But in all cases it is important to recollect that the sand-canal is nothing more than a part of the water-vascular system in which a calcareous deposit has taken place.

Besides all these appendages the circular water-vessel is connected with five vessels, the water-canals, which supply the tentacles and feet and run down the sides of the body in the ambulacral spaces.

The *nervous ring* is formed by a simple cord without ganglionic enlargements, encircling the œsophagus superficial to the water-vascular ring, and giving off five cords which run with, but superficial to, the water-vascular canals in the ambulacral spaces.

The position of the water-vascular canals and of the nervous cords is apparently different in the Asteridæ from what it is in the Echinidæ, inasmuch as in the former these organs are *outside* the bony skeleton, in the latter *inside* it; but this apparent difference arises only from a difference in the mode of development of the ambulacral plates.

The ambulacral plates in the Asteridæ, *between* which the canals lead from the ampullæ to the feet, are homologous with the ambulacral plates in the Echinidæ *through* which they pass.

But in the Asteridæ the ambulacral plates develope internal processes which unite *above*, or internal to, the water-vascular canals and nerves, while in the Echinidæ the ambulacral plates unite *below* or external to the water-vascular canals and nerves.

In the Echinidæ, the only parts that represent the internal processes of the Asteridæ are the "auriculæ"—arched processes which give attachment to the suspensor muscles of the lantern, and under which the vessels and nerves pass.

In the Ophiuridæ both internal and external processes of the ambulacral plates exist, and the vessels and nerves are contained in a complete bony canal.

In the Holothuriadæ the arrangement of parts is as in the Echinidæ. The ring, composed of ten to fifteen bony pieces, encircling the œsophagus, is not homologous with any part of the skeleton of the Echinidæ, but with the lantern or masticatory apparatus.

Five of these pieces are always either notched (as in the Holothuriadæ) or pierced (as in the Synaptæ) for the passage of the water-vessels and nerves, and these pieces correspond homologically with an equal number of calcareous pieces of the lantern of the Echinidæ (falces of Valentin) which cover in the terminations of the radial water-canals in the circular canal.

Every Echinoderm commences its existence as an oval ciliated body like an infusory animalcule, without organs or distinction of parts.

In some genera, such as *Asteracanthion* and *Echinaster*, it appears from the observations of Sars, Agassiz and Desor, that such a germ as this developes at one part one, three, or four short processes or peduncles, by which it is enabled to adhere to other bodies; among these Prof. Müller thinks he has discovered an aperture. The remainder of the germ gradually enlarges and assumes the form of a starfish. The feet appear on its under side whence the peduncle or peduncles proceed. The latter become smaller, and eventually appear as mere processes on one side of the mouth of the young starfish, finally vanishing altogether.

Now in these larvæ, their inner structure and the mode in

which the disc of the starfish is developed do not appear to have been clearly made out, so that points of comparison with the embryological phænomena to be described subsequently are wanting. One thing however appears evident, viz. that, as in the other forms, the axis of the starfish is oblique to the axis of the larva from which it proceeds.

The larvæ whose development has been observed by Prof. Müller are widely different.

These larvæ may be reduced to two kinds: 1st, those of the Ophiuridæ and Echinidæ (fig. 1, 2, 3); 2nd, those of the Asteridæ and Holothuriadæ (fig. 4, 5, 6, 7).

1. The larvæ of the Ophiuridæ and Echinidæ are somewhat hemispherical bodies, having one edge of their truncated side prolonged into a single flat and wide process, which carries the mouth and œsophagus.

On the hemispherical portion—not at the extremity, but on the side opposite to that which is prolonged into the wide process—is a circular anus. The œsophagus leads from the mouth, which looks in the same direction as the anus, and opens into a globular stomach placed in the hemispherical portion of the larva; a short intestine runs from this at right angles with the direction of the œsophagus to the anus.

The extremity to which the mouth is turned may be considered anterior, the anal side inferior, and it is this position which the animal has in swimming*.

In this general description of the form of the larvæ, however, some most important and characteristic features have been omitted. These are, the calcareous rods which form a sort of internal skeleton or framework, and the ciliated fringe which is the organ of locomotion.

The rods are four, eight or more in number; they run forwards, diverging from the most convex or posterior portion of the hemispherical part of the larva, and still clothed by the substance of the larva, form processes of a considerable length: some of them pass through the margins of the hemispherical part of the larva, some run through and support the buccal prolongation†.

The *ciliated fringe* is a sort of ridge, thickly covered with large cilia (which however do not exhibit the wheel motion), which forms the edge of the flat anterior side of the hemispherical part of the larva and of the buccal prolongation. It therefore passes *above* the mouth and before the anus, completely encircling the

* These determinations of anterior and posterior, &c. are altogether different from those of Prof. Müller. The mode of description adopted by the latter is quite accidental, and we have changed it to make the general homologies more clear.

† See the figure given in the 'Annals,' *ante*, vol. xix.

body in an oblique manner. It is continued forwards on one side and back on the other, upon the processes of the calcareous rods, and thereby attains a great length and complicated appearance, but fundamentally its relations are such as have been described. In some of these larvæ Prof. Müller considers that he has detected, in front of and above the mouth, a rudimentary nervous system, consisting of two little ganglia connected by a commissure, whence branches proceed*.

We have described the structure common to all the larvæ of this division; there are certain peculiarities in some, however, which are deserving of notice. Thus in some Echinus-larvæ three long processes containing calcareous rods are developed from the convex posterior extremity of the larva (fig. 3).

In other Echinus-larvæ (fig. 2) these do not exist, but four little prominences, richly ciliated, are developed on the hemispherical portion just where the long processes leave it. These are the "epaulettes" of Müller.

In Ophiurid-larvæ the convex side of the larva bears a circlet of cilia (fig. 1).

2. The second form of larvæ has no internal calcareous skeleton. It falls into two subdivisions: (*a.*) the form of the Holothuriadæ, and (*b.*) the form of the Asteridæ.

a. These larvæ, the *Auricularia* of Müller (fig. 6 & 7), are at first bean-shaped, convex on the dorsal side, concave on the ventral side. An irregular transverse fissure answers to the hilum of the bean, and in this the mouth is placed. The margins of the fissure are edged by a ciliated fringe exactly similar to that of the former kind of larvæ. The anus opens on the ventral surface of the larva, behind the fringe, the posterior portion of which runs between it and the mouth. The fringe forms a continuous circle, the anterior part of which is bent back to form the anterior margin of the fissure in which the mouth lies.

In the course of its growth the margins of the larva and the corresponding parts of the fringe are thrown into numerous lateral processes which give it a scolloped appearance.

The disposition of the intestine, stomach, &c. is as in the first kind of larvæ.

As the larva increases in size and becomes more elongated in form, the primary fringe becomes replaced by a number of ciliated rings which encircle the now cylindrical body of the larva (fig. 7).

b. The Asterid-larvæ.—The *Bipinnaria* (fig. 4), which is the commoner form of Asterid-larva, closely resembles *Auricularia* in its young condition, except that there is a distinct ciliated circle developed upon the surface of the larva in front of the mouth.

* In the Pluteus from Heligoland, but not in other larvæ.

Instead therefore of the anterior boundary of the fissure of the mouth being formed as in *Auricularia* by the recurved anterior part of the "ciliated fringe," it is formed by the posterior part of a distinct band of cilia.

It is particularly to be observed that this "band," like the extra band in the Ophiura-larva, does not encircle the body—it is altogether in front of and above the mouth.

The position of the anus is as in *Auricularia*. A variety of the Asterid-larva, described by Prof. Müller under the name of *Tornaria*, resembles this condition of *Bipinnaria*, but subsequently adds a ciliated ring like one of those of *Auricularia*, which encircles the body near the anal end* (fig. 5).

Bipinnaria increases greatly in size, attaining the length of an inch or more, chiefly by the increase of the anterior part of the body. This assumes a very extraordinary form, both the "band" and the "fringe" throwing out long processes on each side to the number of half a dozen, and at the anterior extremity they form two fin-like expansions placed one above the other.

Another Asterid-larva, *Brachiolaria* (Diag. V.), resembles *Bipinnaria* in general form, but developes three processes anteriorly between the anterior part of the ciliated "fringe" and the anterior ciliated "band."

These are all the forms of Echinoderm-larvæ enumerated by Prof. Müller. Complicated as they seem to be at first sight, it seems to us that they may all be readily reduced to one very simple hypothetical type; having an elongated form, traversed by a straight intestine, with the mouth at one extremity and the anus at the other, and girded by a circular ciliated fringe; just like the larvæ of some Annelids (fig. 9).

Supposing such to be the typical form of the Echinoderm-larva, the specific variations are readily derived from it by simple laws of growth. Let the region before the ciliated fringe be called the *pre-trochal* region, the region behind the fringe be called the *post-trochal* region.

Then the Echinoderm-larvæ would appear to be characterized by a disproportionate development of the dorsal post-trochal region (Diag. I^{a}.) whereby the anus is thrust downwards, and the dorsal part of the ciliated fringe downwards and forwards; processes are then developed from the ciliated fringe as previously described.

As in the Annelid-larvæ patches of cilia are frequently developed elsewhere than in the principal circle, *e. g.* on the sides of the

* If Prof. Müller's conjecture, that his "wurmförmige Larve" (Larven und Metamorphose der Holothurien und Asterien, p. 27) is a further stage of development of *Tornaria*, be correct, it ultimately assumes a still more worm-like shape, and more closely resembles a Holothurid-larva.

body, at the bases of the feet, &c., so in the Echinoderms, ciliated elevations and circles (not encircling the body), and even long processes (*Echinus, Brachiolaria*), are developed upon other parts of the body of the larva than the "ciliated fringe."

In the Echini and Ophiuridæ these additional parts are developed in the post-trochal region (Diag. I. II. III.); in the Asteridæ they are as invariably developed in the pre-trochal region (Diag. IV. V. VI.).

The ciliated circle of the Ophiurid-larva on the dorsal side of the post-trochal region answers precisely to the ciliated "band" on the dorsal side of the pre-trochal region of the Asterid-larva.

We have ventured here to give a general view of the Echinoderm-larvæ different from that put forth by Professor Müller himself, who, we would with all deference suggest, loses sight of the real position of the ciliated fringe in its apparent bilaterality. Speaking of the ciliated fringe he says, "We may name this circular ciliated fringe (Wimper-schnur), to *distinguish it from such as encircle the body transversely*, the *bilateral ciliated fringe*" (Metam. d. Holothurien u. Asterien, p. 35).

We maintain that this "bilateral" fringe itself does, in truth, encircle the body transversely, however distorted it may have become, and the reader is referred to the diagrams for a demonstration of the truth of this position.

A strong confirmation of this opinion is afforded by the structure of the larva of *Sipunculus* described by Max. Müller (Müll. Archiv, 1850, v.). (Fig. 8.)

In this remarkable larva there is a single even band of strong cilia which encircles the anterior part of the animal, and evidently represents the "ciliated fringe" of the other Echinoderm-larvæ. Except that the intestine is bent upon itself, it agrees precisely with our hypothetical type of the Echinoderm-larva.

The Echinoderm-larva, we repeat, may be considered as an Annelid-larva, which has become distorted by the excessive development of the dorsal part of its post-trochal region*.

Out of these larvæ, all of which have a strictly bilateral symmetry, the more or less radiate adult Echinoderms are developed by a process which is a sort of internal gemmation.

Now the result of this process is twofold; either the new

* The only other animals which possess a larva at all resembling that of the Echinoderms and Annelids are certain Trematoda (see Müller, Ueber eine eigenthumliche Wurmlarve aus der Classe d. Turbellarien, Müll. Arch. 1850). Here it would appear that by an excessive development of the pre-trochal region, the ciliated fringe has the concavity of its bend posterior; but the difficulty, from the absence of an anus, of determining the real axis of the body, renders this determination doubtful.

structure ultimately throws off more or less of the larva in which it was developed, or it unites with the larva to form the adult animal, no part being thrown off.

The former is the case in the Ophiuridæ, Echinidæ and Asteridæ, for the most part—the latter in the Holothuriadæ.

The latter process, as the simpler, shall be described first.

A portion of the dorsal integument of the larva becomes as it were thrust inwards (fig. 10.) towards one or other side of the stomach, as a tube terminated by an enlarged globular extremity, whose cavity communicates with the exterior and is ciliated internally.

The vesicle which terminates this "internal bud" now sends forth processes so as to form a sort of "rosette," which lies close to and above the stomach.

The "rosette" becomes a circular canal (the circular canal of the water-vascular system), from which cæca are given off anteriorly to form the tentacles, posteriorly to the parietes, in which they become the water-canals.

The former mouth of the larva is obliterated, and a new one is formed in the centre of the circular canal and its tentacular appendages. This is the permanent mouth of the Holothuria, which is therefore *a new structure formed upon the dorsum of the larva.*

In the meanwhile, vesicles, the Vesiculæ Polianæ, are developed from the circular canal, and a deposit of calcareous matter takes place round a portion of the tubular canal, from whose spherical extremity the water-vascular system has been formed. That portion of the tubular canal which lies between the dorsal parietes and the calcareous deposition dies away, and the remainder hangs freely from the circular canal of the water-vascular system as the "sand-canal."

The process in the Echinidæ, Asteridæ, and Ophiuridæ is essentially the same; only, as in these the old body is to be more or less completely discarded, the development of the water-vascular system is attended, *pari passu*, by that of a mass of cells from which the new body is to be formed.

We cannot do better than adduce in illustration Prof. Müller's description of the development of the Echinoderm in the Asterid-larva *Bipinnaria* (Fortsetzung der Untersuchungen über die Metamorphose d. Echinodermen, Müll. Archiv, 1850).

In larvæ which are not 0·15 of a line in length, the dorsal pore and the tube which proceeds from it are perceptible. It passes into a longish sac, in which, as in the tube, there is a ciliary motion. The sac lies behind, at the side of the œsophagus (Diag. IX.).

Soon after the appearance of these parts, a hyaline mass, in which

very small cells are imbedded, is seen lying like a mantle upon the dorsal side of the stomach.

The sac becomes developed into a rosette of five cæca, the first foundation of the water-vascular system.

The mantle-like mass curves over and covers in the stomach and foundation of the tentacles like a cap, widely open below. The dorsal pore becomes invested by it, and it extends round the anus; but the œsophagus remains outside it (Diag. XI.).

A crest or elevation now appears on the mantle-like mass, and runs obliquely over it in a curved line, whose ends become eventually united. It then forms the margin of the starfish.

What lies beneath this thickened margin belongs to the dorsum of the starfish, what lies above it to its ventral surface.

The young starfish now attains a diameter of $\frac{1}{7}$th of a line, becomes slightly pentagonal, and retains only a narrow connexion with the *Bipinnaria*.

The digestive canal, and with it the rosette-like rudiment of the water-vascular system, becomes turned so as to present the latter towards the ventral surface of the starfish, at that point where its mouth is subsequently formed. The tube which connected the rosette with the pore, which is now imbedded in the dorsal surface of the starfish, receives a calcareous deposit and becomes the sand-canal, while the "pore" is converted into the madreporic plate.

The œsophagus of the larva is obliterated, whilst its rectum projects as an anal tube subcentrally from the dorsal surface of the starfish (Diag. XIII.).

The slightest touch now separates the starfish from the larva in which it was developed; the former sinks to the bottom and creeps by the aid of its newly-developed feet; the latter swims about as before for some time, but eventually perishes.

In the Echinidæ the process is essentially the same. An internal diverticulum of the integument of the larva is formed, but from a somewhat different spot*, namely in front of the ciliated fringe and on one side. It is connected with a vesicle which lies close against the œsophagus, and from which the water-vascular system is developed.

At this place the shell of the *Echinus* subsequently makes its

* It is remarkable that in the Asterid-larvæ, while the development of accessory ciliary processes, &c. takes place in the pre-trochal dorsal region, the bud of the Echinoderm is developed from the post-trochal region. In the Echinus-larvæ we have just the reverse—the bud is developed from the pre-trochal region ("below the lateral arch of the ciliated band," Müller), while the processes, &c., as we have seen, are developed from the post-trochal region. The Ophiuræ appear to present the same relations as the Echinidæ, though Prof. Müller has not been able to make out the point with certainty.

appearance as a circular disc, which gradually envelopes the stomach, and developes tentacles and spines. A new anus is formed as well as a new œsophagus, in the young sea-urchin.

The development of the Ophiuridæ has not been traced so far back as that of the other groups. The dorsal pore and tube have not been observed; but the development of the "rosette" and its accompanying mass of cells into the Echinoderm takes place as in the Asteridæ.

The observations of Dr. Busch (Müll. Arch. 1849) have shown that the larva of *Comatula* very early assumes the form of the Holothurid-larva with ciliated rings, but its internal structure and the development of the Echinoderm are not understood.

To sum up, in Prof. Müller's words, the variations of the metamorphosis of Echinoderms:—

"1. The change of the bilateral larva into the Echinoderm takes place when the larva yet remains an embryo, and is universally covered with cilia, without a ciliated fringe. A part of the body of the larva takes on the form of the Echinoderm; the rest is absorbed by the latter. (A part of the Asteridæ, *Echinaster, Asteracanthion,* Sars.)

"2. The change of the bilateral larva into the Echinoderm takes place when the larva is perfectly organized; that is, possesses digestive organs and a special ciliated fringe. The Echinoderm is constructed within the Pluteus like a picture upon its canvass, a piece of embroidery in its frame, and then takes up into itself the digestive organs of the larva. Hereupon the rest of the larva vanishes * (*Ophiura, Echinus*), or is thrown off (*Bipinnaria*).

"3. The larva changes twice. The first time it passes out of the bilateral type with lateral ciliated fringe into the radial type, and receives instead of the previous ciliated fringe, new locomotive larval organs, the ciliated rings. Out of this pupa-condition the Echinoderm is developed without any part being cast off (*Holothuria,* some Asteridæ).

"If we call embryonic type the condition in which the animal leaves the egg, and when the internal organs are not yet developed, we have four stages or types—the embryonic type, the larval type, the pupa type, and the Echinoderm type. The animal may pass from either of the first three forms into the Echinoderm, or may run through them all." (Larven u. Metam. d. Holoth. u. Asterien, p. 33.)

Furthermore it may be stated that the nature of the change

* It seems questionable how far the integument of the larva over the Echinoderm can be said to vanish, when it is remembered that the pedicellariæ are developed thereon while the Echinoderm is still quite rudimentary.

here called development of the Echinoderm, is, that a process of the integument of the larva grows inwards and lays the foundation of the future water-vascular system, on which the other organs of the Echinoderm, whether nervous, vascular or tegumentary, are in a manner modelled*.

It is of very great importance to remember this fact in considering the homologies of the parts of the Echinoderms.

If the larva of the Echinoderm pursued its normal course of development, it is obvious that its nervous system, for instance, would be homologous in form and position with that of other Annulose forms. There would be a ring with cerebral ganglia round the œsophagus and a chain of ganglia proceeding therefrom, if the nervous system were of the type of the Annelids. Or if it resembled that of the Trematoda, there would be an œsophageal ring with two opposite ganglia, from which a cord would proceed on each side of the body. But the nervous system of the adult Echinoderm can be reduced to neither of these types; it consists invariably in the Ophiuridæ, Asteridæ, Echinidæ, and Holothuriadæ, of a circular or pentagonal cord surrounding the œsophagus (*of the Echinoderm*) without distinct ganglia. From this five cords proceed, in a perfectly radiate manner, following the course of the water-canals.

The study of development renders the reason of this discrepancy obvious. The œsophagus of the Echinoderm is not homologous with the œsophagus of the larva, nor with the œsophagus of an Annelid, and therefore the nervous ring of the Echinoderm is not homologous with the nervous ring of the Annelid. Indeed, since the mouth of the Echinoderm answers homologically to an aperture in the dorsal wall of the stomach of the larva, and since the nervous system of the Echinoderm follows exactly in its form the form of the water-vascular system of the Echinoderm, which is essentially a process of the dorsal integument of the larva, we might be tempted to conclude that the nervous system of the Echinoderm is homologous, not with the ordinary ganglionic chain of an Annelid, but with that elaborate system of dorsal-proboscidean nerves which M. Quatrefages has detected and described in the latter.

The fact that these nerves supply eye-spots would indeed present some difficulties in the way of this hypothesis, if this system of nerves in the Annelida is truly stomatogastric. But in the first place it has not been shown so to be; and in the second place, the existence of well-organized eyes supplied by nerves from the ordinary ventral ganglia in each segment of *Poly-*

* Hitherto we have chiefly quoted Prof. Müller, but for what follows we must be considered alone responsible, unless direct mention be made to the contrary.

ophthalmus, would lead us to hesitate in drawing any very strict conclusions from position and structure to function, in the nervous system of these animals *.

Yet one word upon the bearing of the facts of development now made known, on the affinities of the various groups of Echinoderms.

If we were to arrange the Echinoderms according to the nature of their larvæ, we should have one group formed by the Asteridæ, Holothuriadæ and Crinoideæ (*Comatula*); and another composed of the Ophiuridæ and Echinidæ. And if the acute speculation of Prof. E. Forbes, that the pectinated rhombs of the Cystideæ answer to the "epaulettes" of the Echinus-larva, be correct, then the Cystideæ would, as a sort of permanent form of Echinus-larva, fall into the latter group, in which they would represent the Crinoideæ.

Interesting as are the phænomena presented by the larvæ of the Echinoderms, taken in themselves, as mere facts, they are far more important in their bearing upon one of the most comprehensive and interesting zoological theories of modern times—we refer to the theory of "the alternation of generations." Founded by Chamisso and Eschscholz, extended to a great number of new cases by Steenstrup, and finally reduced to a fixed and definite scientific form under the name of "Parthenogenesis" by the celebrated Hunterian Professor of Comparative Anatomy, this theory has bid fair to unite all the aberrant generative processes of the Invertebrata (those of the Echinoderms among the rest) under its conditions, and to express them in its terms.

The theory may be generally expressed thus: 1. The ovum produces an individual A^1, whose offspring is another individual B dissimilar to A^1. This again may in the same way produce an individual C, and so on. The last of the series only contains generative organs from which ova are formed, and these reproduce an individual A^2 precisely resembling A^1. The species therefore is said to be represented by a number of generations of individuals which regularly alternate with one another.

To this Professor Owen adds—

2. That the individuals B, C, D, &c. which intervene between the sexual individuals A^1 and A^2 are always developed from masses of cells which are the immediate and unchanged descendants of the embryo cells of the ovum, and which as such, retain a portion of the original "spermatic force," whence they are enabled to attain a certain independent development without a renewal of the spermatic influence.

* Again, the eyes of the Acephala are as much supplied from the palleal or visceral ganglion as from the cerebral ganglion.

Now the questions to be decided before the alternation theory can be said to apply to the Echinoderms or any other animals, are different as regards the two portions of the theory. The problem as regards the first question is a matter of naming—as regards the second it is a matter of fact.

We have said that the question involved in the first part of the theory is a question of naming. It is, whether we can apply to A, B, C, &c. in the foregoing instance, the name "individual." For it is quite clear that if they cannot with propriety be called "individuals," their succession cannot be called an "alternation of generations," inasmuch as generations are composed of individuals.

We must carefully bear in mind that this inquiry has nothing to do with the thorny problem of psychical individuality. With that the zoologist has no concern; his science investigates the laws of animal form, and in psychological questions he has no more *direct* interest than the astronomer has in the zoology of the planet Saturn.

Leaving psychological considerations aside, then, and inquiring into the *zoological* meaning of the term "individual," we find that anything to which it is applied among the higher and the greater part of the lower animals, has two principal characters: first, it has an independent existence; and secondly, it is the total result of the independent development of a single ovum.

Now the forms A, B, C, described as "individuals" by Steenstrup, have only one of these characters (in the most strongly marked cases of "alternation"), that of independent existence; for each of them is only *part* of "the total result of the development of a single ovum."

But in predicating "individuality" of any animal which does not "alternate," we predicate both these characters of it.

Hence, unless the meaning of the term "individual" be altered, the advocates of the alternation theory commit the capital error of using the same term in two very different senses, according as they speak of a Hydra or a Campanularia, a Salpa or a Cynthia.

It is only by narrowing the meaning of the word "individual" to mere "independent existence," that it can possibly become applicable in Steenstrup's sense. But in this case spermatozoa, spermatophora, and even cancer cells, would equally be "individuals." So that the new meaning would be not only entirely arbitrary, but opposed to the general sense of zoologists.

We propose on the other hand not to alter the ordinary zoological meaning of the word "individuality," but merely to define it more strictly, and give to the relative value of the attributes which it connotes, and which are conversely a mark of it.

Individuality has so long and so obviously, among the higher animals, been observed to be accompanied by independent existence, that the latter attribute has come to be considered as, conversely, an indication of individuality—to the neglect of the really characteristic attribute, which is—the circumstance of being the total result of the development of a single ovum.

According to our view, then, the zoological individual = the total result of the development of a single ovum, whether this total result consist of one or many independent existences. The individual is the zoological unit, and its value is the same, whether we have it as (1) or as $(\frac{1}{3}+\frac{1}{3}+\frac{1}{3})$. A fraction does not become equal to the unit by standing alone. The Cyanæa and the Polype from which it proceeds, the two forms of Salpæ, the parent nurses, nurses, and Cercariæ, of the Distomata, are not distinct individuals—are not separately equivalent to an individual beetle or dog.

It is their sum only, which is equivalent to the individual among the higher animals.

They are not the individual, but are successive forms by which the individual is manifested; standing in the same relation to the individual, as the incarnations of Vishnu to Vishnu, in the Hindoo theology.

What then may these independently existing "parts of individuals" be properly termed? They can hardly be called organs, without doing violence to our ordinary acceptation of the nature of an organ, in which a certain subserviency and dependence is understood. The term "*zooid*" has been devised; and as it has no theoretical meaning, but is merely intended to suggest two indisputable facts with regard to the creatures to which it is applied—namely that they are like individuals, and yet are not individuals, in the sense that one of the higher animals is an individual—its use does not appear to be open to any serious objection.

Instead of saying then, that in a given species, there is an alternation of so many generations, we should say that the individual consists of so many zooids.

Again, where no "alternation" takes place, the individual = the sum of its organs; where there is alternation, the individual = the sum of its "zooids."

If the view we have taken be correct, the whole doctrine of the so-called "compound animals" must be revised, and their terminology altered. A whole tree of Sertularia, a Pennatula, a Pyrosoma, a mass of Botrylli, must no longer be considered as an aggregation of individuals, but as an individual developed into many zooids.

And if the term "compound animal" is to be retained in its

old meaning, we know of only one creature which is entitled to the name, viz. the *Diplozoon paradoxum*, which Von Siebold has just shown to be really formed by the fusion of two previously distinct individuals.

We hope that the reader will pardon this long digression into the regions of abstract thought. Whether he adopt our view or not, we trust that at any rate, we have pointed out where the real battle of the alternation theory lies.

The onus of giving a new meaning to the word "individuality" must rest with the advocates of the alternation theory; we have endeavoured merely to make a consistent extension of the old meaning to embrace new facts.

The Echinoderms have been included under the "Alternation theory;" but, if the reasoning above be correct, unjustly, as is indeed plainly pointed out on other grounds by Prof. Müller in his second memoir. He justly observes that the process of development of the Echinoderm partakes as much of the nature of metamorphosis as of "alternation." The larva and the Echinoderm cannot be said to be two individuals, when they possess the same intestine.

Nor, as to the question of fact, does the development of the Echinoderm appear to be a case of "Parthenogenesis."

The structure of the integument of the larva, at the place where the tubular rudiment of the Echinoderm is subsequently formed, is quite undistinguishable from that of any other spot. There are here no descendants of the embryo-cells specially set aside to become developed into the new structure*.

The development of the Echinoderm is then neither a process of "alternation of generations" nor of "Parthenogenesis," but the individual consists of two zooids—a larva-zooid and an Echinoderm-zooid, the latter of which is developed from the former by a process of internal gemmation†.

* The elongated cellular masses which exist on each side of the digestive canal in the larvæ, are very possibly the immediate descendants of the embryo-cells. But Prof. Müller leaves it very doubtful, whether these masses have anything to do with the development of the Echinoderm. Certainly they are not concerned in the development of one most important part of it—the water-vascular system. See Müll. Arch. 1850, p. 466. *Ibid.* 1851, p. 4.

† According to Prof. Müller (Archiv, 1851, p. 18) the development of the Echinoderm can only "figuratively" (bildlich) be compared to gemmation, inasmuch as the "formative mass" arises independently.

But since he says immediately afterwards that "the rudiment of the water-vascular system, in general, arises before the rudiment of the parietes of the Echinoderm," and since he shows elsewhere that the origin of the water-vascular system is by the development of a bud-like process inwards —the process may, we think, be called gemmation in much more than a figurative sense.

The development of the Echinoderms is, as Prof. Müller observes, exactly intermediate between the ordinary process of metamorphosis by ecdysis in insects and the so-called "alternation" of the Trematoda and Aphides.

The phænomena of alternation, or as we have called it, "zooid development," take place in two ways—by external gemmation and by internal gemmation.

The former process is confined to the Polypes and Ascidians, which form a series leading from the lowest Radiate to the Molluscous types. The latter process on the other hand is restricted to the Worms and Echinoderms, which form a series leading from the lowest Radiate to the Annulose types.

Now in each series three modifications may be detected. The deutero-zooid is developed either—1. from a complete segment of the protozooid, when it is difficult to say whether the process is one of internal or external gemmation; or 2. from a small portion of a segment, including a portion of the digestive canal; or 3. from a small portion of a segment, an entirely new digestive canal being formed.

The following table will illustrate the relations of these modifications to one another :—

	Zooid Development by	
	External Gemmation.	*Internal Gemmation.*
3.	Salpa	Aphides. Trematoda.
2.	Campanularia Corynidæ, &c.	Echinodermata.
1.	Cyanæa. Tænia. Nais.	

We have hitherto considered the various zooids of each form to be complementary to one another, and all necessary to the perfect manifestation of the individual.

But the law of "irrelative repetition" long since established elsewhere by Prof. Owen, is illustrated here in the development of zooid forms where they are not necessary to the manifestation of the individual.

In the Echinoderm there is one larval-zooid and one Echinoderm-zooid—the "individual" would be incomplete without either.

But in the Cyanæa the single Scyphistoma-zooid developes perhaps twenty Cyanæa-zooids, any one of which would have been sufficient to complete the individual.

The development of the hundreds of polypes of a Sertularian appear to be referable to a similar law. Nay, the "generation

by gemmation" of a Hydra or a simple Ascidian, and the fission of a Microstomum, seem, strictly speaking, to be phænomena of the same kind.

As in these cases, however, it is impossible when once the gemma is separated from the parent stock to distinguish it from a true individual, it may seem pedantic and unnecessary to insist upon the distinction.

In concluding, we cannot refrain from remarking upon one character of Professor Müller's researches, of which our imperfect notice can give no idea,—it is the singular candour and philosophic impartiality of the writer. In the course of five years, much that seemed probable at first, had, later, to be rejected—much that seemed certain, to be overthrown. It was often necessary to make pretty hypotheses give way before stubborn facts—to re-examine conclusions that had seemed unquestionable.

If any one be curious to know how this has been done, and desire at the same time to learn in what spirit scientific investigation should be conducted, we cannot do better than refer him to the works whose titles head this Report—they are models.

EXPLANATION OF PLATE I.

The figures numbered with the Arabic numerals all represent really existing forms, and are taken, with the exception of figures 8 and 9, from Professor Müller's memoirs. The "calcareous rods" are omitted for the sake of clearness.

The figures numbered with the Roman numerals on the other hand are all to be considered merely as diagrams. They represent what the Echinoderm-larvæ would be if they were, as it were, straightened out and reduced to their simplest elements.

Fig. I.[a] is given in order to show how a symmetrical Annelid-like larva, fig. I., may by development of some of its parts at the expense of others become converted into the Ophiura-larva, fig. 1.

Fig. 1. Ophiura-larva	I.	The corresponding diagram.
Fig. 2. Echinus-larva with "epaulettes"	II.	Ditto.
Fig. 3. Echinus-larva with spines viewed from behind.	III.	Ditto.
Fig. 4. Asterias-larva (*Bipinnaria*), very young.	IV.	Ditto.
Brachiolaria, an Asterias-larva...	V.	The diagram only is given.
Fig. 5. *Tornaria*, probably an Asterias-larva.	VI.	The corresponding diagram.
Fig. 6. *Auricularia*, the Holothuria-	VII.	Ditto.
Fig. 7. larva in its two forms	VIII.	

In all the figures of larvæ the mouth and anus are indicated by the letters *m* and *a*, and the cilia are disproportionately large so as to render the "fringes" and "bands" evident.

The Diagram No. I. is similarly lettered, and all the other diagrams have their anterior and posterior extremities in a position corresponding to it.

Fig. 8. is the larva of *Sipunculus* after Max. Müller.
Fig. 9. The larva of an Annelid after Milne-Edwards.
Fig. 10. *Auricularia.* The larva of Holothuria, after Müller; to show the mode of development of the water-vascular system, &c. from the internal bud, *d*: *e*, the oval masses of cells.
Fig. 11. One of the epauletted Echinus-larvæ, in which the Echinoderm, *d*, has already begun to envelope the stomach of the larva.

IX. X. XI. XII. XIII. are diagrams intended to represent the mode of development of an Asterias within its larva the *Bipinnaria*.

The form of the latter is not given; its relation being indicated only by the dotted line.

IX. *m*, the mouth of the larva; *a*, its anus; *d*, the bud-like commencement of the Echinoderm.
X. XI. The latter has developed the water-canals, and with its accompanying blastema has begun to invest the stomach of the larva.
XII. The investment nearly complete. The position of the mouth of the Asterias indicated by (*o*).
XIII. The Echinoderm has become free and separate from the body of the larva with its primitive œsophagus.

It is to be understood that these diagrams do not pretend to be strictly accurate. They are intended only to render the process of development more easily comprehensible.

II.—*Report on* MM. L. R. *and* C. Tulasne's "*Memoir on the History of the Hypogæous Fungi.*" By MM. Jussieu and Ad. Brongniart*.

The mode of vegetation and reproduction of the Fungi had long been one of the most obscure portions of the vegetable kingdom, and, in spite of the progress of this department of botany during the last fifty years, many points yet remain to be cleared up; but in this vast class, the anomalous organization of which has caused some naturalists to regard them as a kind of peculiar kingdom, nothing perhaps is more singular than the development of the subterranean Fungi, the whole life of which, the growth and reproduction, goes on in the bosom of the earth, without any portion of their structure coming to the surface.

This existence, entirely removed from the action of light, is an anomaly even among the plants of the Fungous class, which, generally speaking, prefer weakly illuminated situations; for ordinary Fungi cannot live in complete obscurity without becoming profoundly altered in form and structure, and being kept imperfect and sterile. Light therefore, although in less degree necessary to Fungi than to ordinary vegetables, is almost always indispensable to their regular development at least at the period of reproduction.

For a long period the common Truffle, and a few other equally

* Comptes Rendus, Dec. 30, 1850.